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Pleurobranchaea inconspicua* Bergh, 1897 (Opisthobranchia: Pleurobranchidae): Redescription and distribution from Argentina and Colombia

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Abstract. A taxonomic study based on fresh specimens from Argentina and Colombia, and voucher material from the collections of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN) and Museo de Historia Natural Marina de Colombia (MHNMC-INVEMAR) was conducted. The first study by scanning electron microscopy (SEM) of the radular, jaw elements and reproductive anatomy, paying special attention to the internal cuticular stylet of the penis, is presented. Previous descriptions of *P. inconspicua* and its junior synonyms, *P. hamva*, *P. hedgpethi*, and *P. gela*, are compared with the present results; *P. bonnieae* is synonymized and a checklist of the distinguishing features of relevant species within the genus *Pleurobranchaea* is provided. This work aims at discussing the proposed amphiatlantic distribution of *P. inconspicua* and at solving the problems of synonymies. It provides a starting point for a comparative study of specimens of the genus *Pleurobranchaea* from both sides of the Atlantic Ocean and the Mediterranean Sea that will be complemented with molecular studies in future times.

Keywords. Taxonomic redescription, Colombian Caribbean, Argentina, amphiatlantic distribution.

1. INTRODUCTION

The genus *Pleurobranchaea* Meckel in Leue, 1813 is represented in temperate-warm waters, by several species with wide geographical distribution ranges. *Pleurobranchaea inconspicua* Bergh, 1897 was described from northern Brazil (type locality: Sergipe, 10° 54' S, 37° 7' W), and its distribution was later extended under the same name or under junior synonyms of species and subspecies to several localities in the Western Atlantic Ocean (USA, Caribbean, Brazil, Argentina) and to localities more distant from the type locality, such as the Mediterranean Sea (Israel) and West Africa (Ivory Coast to Nigeria).

MARCUS & GOSLINER (1984) gave the most recent revision of the subfamily Pleurobranchaeinae, which included 14 species of the genus *Pleurobranchaea*. However, these authors did not include the species *P. morosa* Bergh, 1892, *P. morula* Bergh, 1905, *P. melanopus* Bergh, 1907, *P. algoensis* Thiele, 1925, *P. japonica* Thiele, 1925, and *P. dorsali* Allan, 1933, because they were poorly described. Nevertheless, *P. japonica* was redescribed by TSUBOKAWA et al. (1992), confirming the validity of the species and *P. morosa* has been recently mentioned from Azorean archipelago by MALAQUIAS (2001) and CERVERA

et al. (2006), although both works refer to the original description only.

In MARCUS & GOSLINER's revision (1984), the names *P. hedgpethi* Abbott, 1952, *P. hamva* Marcus and Marcus, 1955 (misspelled *hamwa*) and *P. gela* Marcus and Marcus, 1966 were considered junior synonyms of *P. inconspicua*. ABBOTT (1952) described *P. hedgpethi* from Port Aransas (Gulf of Mexico); this species became the most frequently mentioned junior synonym of *P. inconspicua* for the Western Atlantic, even more frequently than the senior synonym. However, in the same revision, these authors erected the species *P. bonnieae* for one specimen from Florida region. According to VALDES et al. (2006) this name could be another junior synonym of *P. inconspicua*.

Several authors considered the anatomy of the reproductive system and the penial morphology as the most useful characters to discriminate species of the genus *Pleurobranchaea* compared to the classical hard structures of radulae and jaws (MARCUS 1961; MARCUS & GOSLINER 1984; WILLAN 1987).

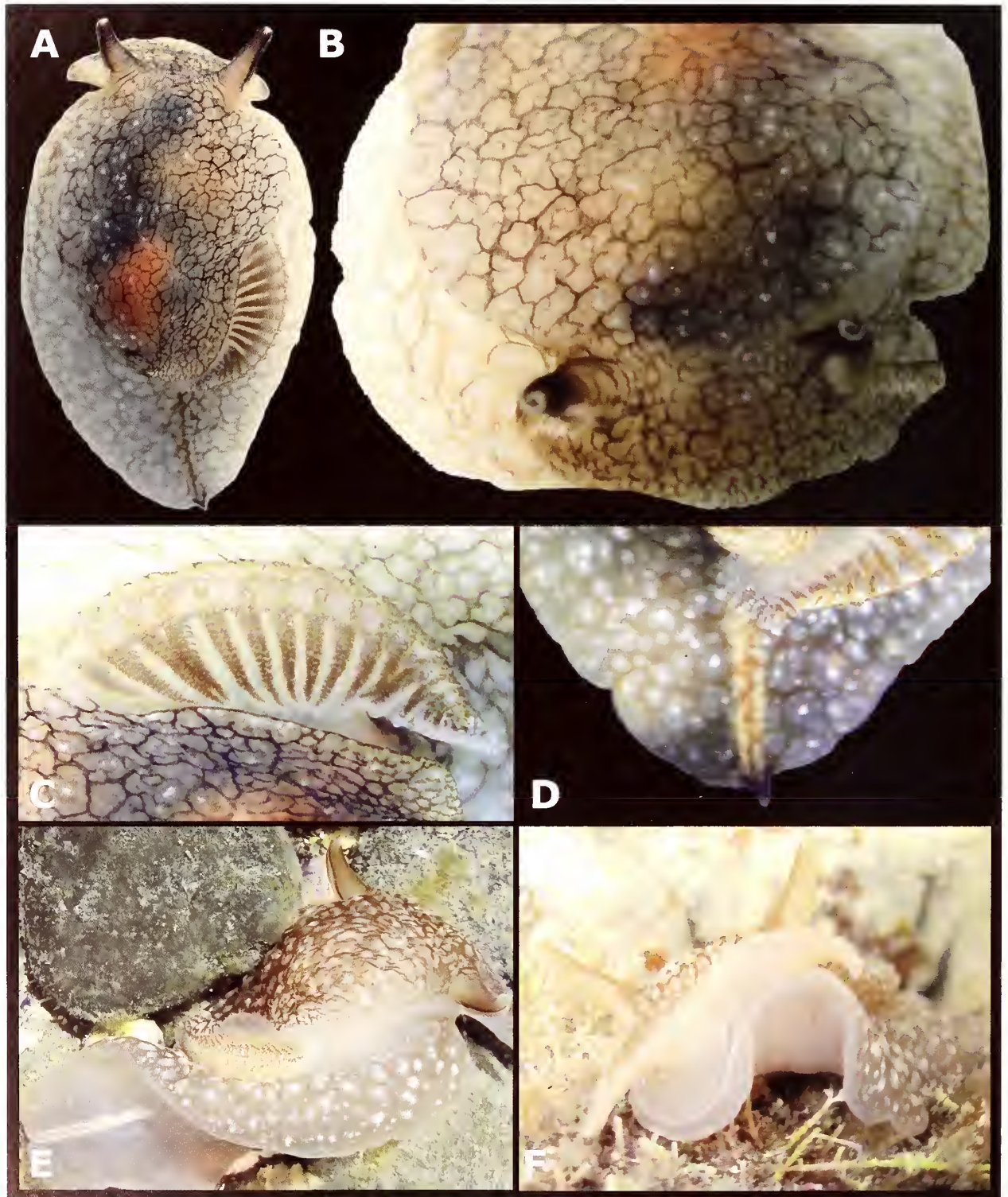


Fig. 1. *Pleurobranchaea inconspicua* Bergh 1897. A. Dorsal view of living specimen from Colombia (Photo: N. Ardila). B. Dorsal view of head. C. Detail of the gill and the pairs of pinnules. D. Foot showing a conspicuous spur. E. Living specimen from Patagonia (80 mm length) (Photo: C. Muniain). F. Detail of rhinophores and sensory papillae on the oral veil (Photo: C. Muniain).

Unlike most of the previous descriptions of *P. inconspicua* and of other species of the genus conducted from preserved material, often in bad conditions, this work re-describes the characteristics of recently collected specimens of *P. inconspicua* from two distant localities.

This is the first study using SEM for hard structures of *P. inconspicua*, especially the examination of the penial stylet. Detailed descriptions of the external appearance and the hard structures, as well as the reproductive system, of specimens from distant localities help to understand the intraspecific variability in this species, and allow to discuss the possible amphiatlantic distribution of *P. inconspicua* by comparison with material from other Atlantic localities. Here, synonymization of other *Pleurobranchaea* species with *P. inconspicua* is outlined.

2. MATERIALS AND METHODS

Specimens were collected over a wide range of depths from shallow intertidal areas down to 150 m in depth. A total of 16 specimens were preserved in 70% ethanol. Photographs and videos were obtained with a digital camera from living specimens. Part of this material is deposited in the Museo de Historia Natural Marina de Colombia (MHNMC-INVEMAR) as well as in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN).

Colombia: Four specimens collected with a bottom trawl (9 x 1 m opening, 16 m in length) during the research cruises INVEMAR-MACROFAUNA II, 2001 aboard the R/V Ancon, in the Caribbean coast of Colombia at 70 and 150 m depth; two specimens off Dibulla (11° 25' 34"N, 73° 27' 40"W), E-100, 150 m depth (MHNMC-INVEMAR: 3872, 3873), two specimens off Buritaca (11° 18' 28"N, 73° 46' 50"W) E-108, 109, 70 m depth (MHNMC-INVEMAR: 3874, 3875). One specimen was collected by SCUBA from Neguanje Bay, 5-10 m depth in a culture of bivalves (Ardila priv. coll.).

Argentina: One specimen from Puerto Quequén (38° 34'S, 58° 38'W) Buenos Aires, 12/1928, MACN-in: 18234; one specimen from Puerto Quequén, Buenos Aires, 2/1929, MACN-in: 18312; two specimens from Puerto Quequén, Buenos Aires, 1/1934, MACN-in: 412; six specimens from Creek Bay (41° 6'S, 63° 56'W), San Matías Gulf, Río Negro, MACN-in: 36985; one specimen from Larralde (42° 25'S, 64° 19'O), San José Gulf, Chubut, 10/1/2006, MACN-in: 37064.

Two specimens were dissected, and their jaws and radulae were removed and mounted for Scanning Electron Microscopy (SEM) examination (MACN-in: 36985, 37064).

Two penises and their respective cuticular stylets were previously critical-point-dried for SEM (MACN-in: 36985, 37064).

3. RESULTS

3.1. Systematic description

Nudipleura Wägele & Willan, 2000

Pleurobranchoidea Gray, 1827

Pleurobranchidae Gray, 1827

Pleurobranchaeinae Pilsbry, 1896

Pleurobranchaea Meckel in Leuc, 1813 (type *Pleurobranchidium meckelii* Blainville, 1826)

Pleurobranchaea inconspicua Bergh, 1897 (Figs 1–5)

Pleurobranchaea inconspicua Bergh, 1897 (BERGH 1897: 49–51, pl. 8, figs 2–10. MARCUS & GOSLINER 1984: 24–27, figs 1B, 10–11. RÍOS 1984: 206–207, pl. 69, fig. 987. MUNIAIN 1997: 4, 17, 34. ARDILA & RACHELLO 2004: 62, fig. 3).

Pleurobranchaea hedgpethi Abbott, 1952 (ABBOTT 1952: 1–2, pl. 1, figs 1–8. MARCUS & MARCUS 1959: 253 fig. 6. MARCUS & MARCUS 1960: 253–254, fig. 6. NIJSSEN-MEYER 1965: 143–145, figs 1–2. MARCUS & MARCUS 1967a: fig. 55C. MARCUS & MARCUS 1967b: 200. MARCUS & MARCUS 1969: 18. ABBOTT 1974: 348, fig. 4201.

Pleurobranchaea hamva Marcus & Marcus, 1957 (MARCUS & MARCUS 1957: 21–27, figs 40–52).

Pleurobranchaea hedgpethi hamva Marcus, 1961 (MARCUS ER. 1961: 141. MARCUS & MARCUS 1967a: 48).

Pleurobranchaea gela Marcus & Marcus, 1966 (MARCUS & MARCUS 1966: 174, figs 35–37).

Pleurobranchaea bonnieae Marcus & Gosliner, 1984 (MARCUS & GOSLINER 1984: 29–32, figs 1D, 13–14.).

3.1.1. External features

Length of the living animals ranges between 13 and 80 mm. The body is oval and elongate. The ground colour is pale cream, with a dense dark brown reticulate along the mantle dorsal region, being lighter and less obvious in the foot dorsal region and absent in the well developed rhinophores (Fig. 1A, B, E). Bright white spots are scattered all over the mantle and more conspicuous on the dorsal foot surface. The oral veil is broad with sensory papillae along the anterior edge. Rhinophores are held erect in the living animals (Fig. 1B, F), whereas in the preserved ones they are in a lateral position.

The mantle is reduced and fused with the oral veil; a large gill is visible on the right side of the body. The gill is attached along most of the body with about 26 pairs of pinnules per gill (Fig. 1 C, E). The anal papilla lies over the seventh pinnule. The foot is rounded in front. The soft mantle, not covering the foot, is visible to most of its part (Fig. 1 A, E). The coloration in the ventral foot region is translucent, and the internal organs can be observed by transparency. At the posterior end, the foot ends in a rounded shape, with a large metapodial gland (yellowish) extending longitudinally from the posterior mantle towards the central foot sole (Fig. 1 E). Dorsally to the metapodial gland, the foot has a brown or black tiny spur (Fig. 1 A, D).

3.1.2. Anatomy

A shell is lacking. The pharyngeal bulb frequently protruded in preserved specimens through the eversion of the very extensible oral tube. Jaws consist of two paired and elongate chitinous plates on the lateral walls of the pharyn-

geal bulb. The radular formula of one specimen of 40 mm in life is 30 X 64.0.64 (MACN-in: 36985). The radula lacks a rachidian tooth, but a difference among the first four laterals is noticeable in some radular rows (Fig. 2A). Lateral teeth are bicuspid, largest in the middle of the half-row and smaller towards the outer border (Fig. 2B). The jaw elements (rodlets) bear 4 to 8 denticles from the outermost and innermost region (Figs 2C, D).

The reproductive system arrangement is similar to that of other *Pleurobranchaea* species (Fig. 3). The tubular ampulla forks near its outlet into two branches, the shorter branch is the oviduct that enters the capsule gland, and the other branch is the efferent duct that splits in two. One branch enters the prostate and then continues within the penial sac (Fig. 3, number 4). The second branch leads to the bilobed seminal receptacle, which is connected to the bursa copulatrix by a long and thin convoluted duct. The bursa copulatrix is large and round.

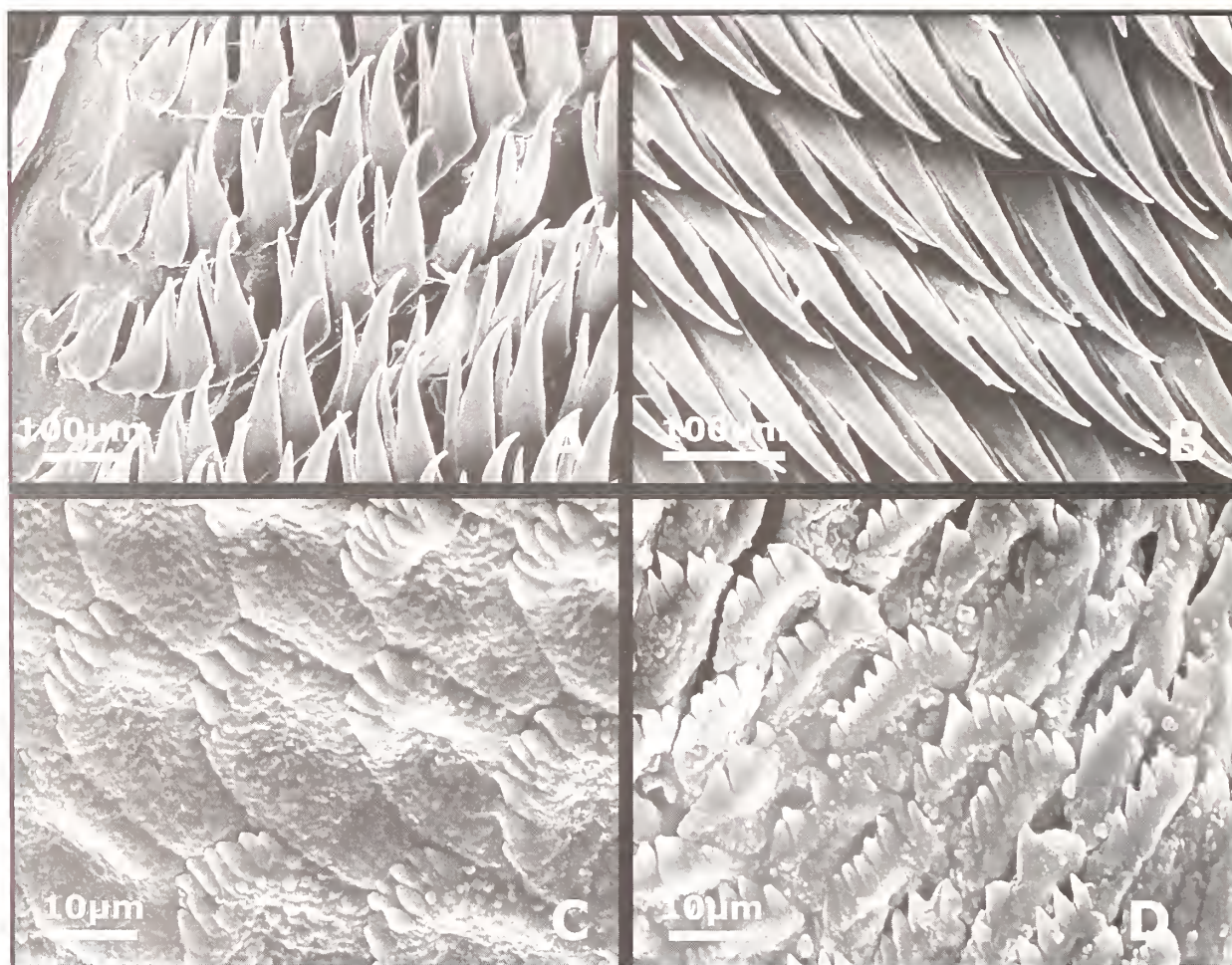


Fig. 2. A–D. Scanning electron photographs of radula of *P. inconspicua* MACN-in: 36985. A. Radula lacking a rachidian central tooth. B. Outermost teeth on the same radula side (right). C, D. Jaw showing platelets with 4–8 denticles from outermost region. D. Jaw showing platelets from innermost region.

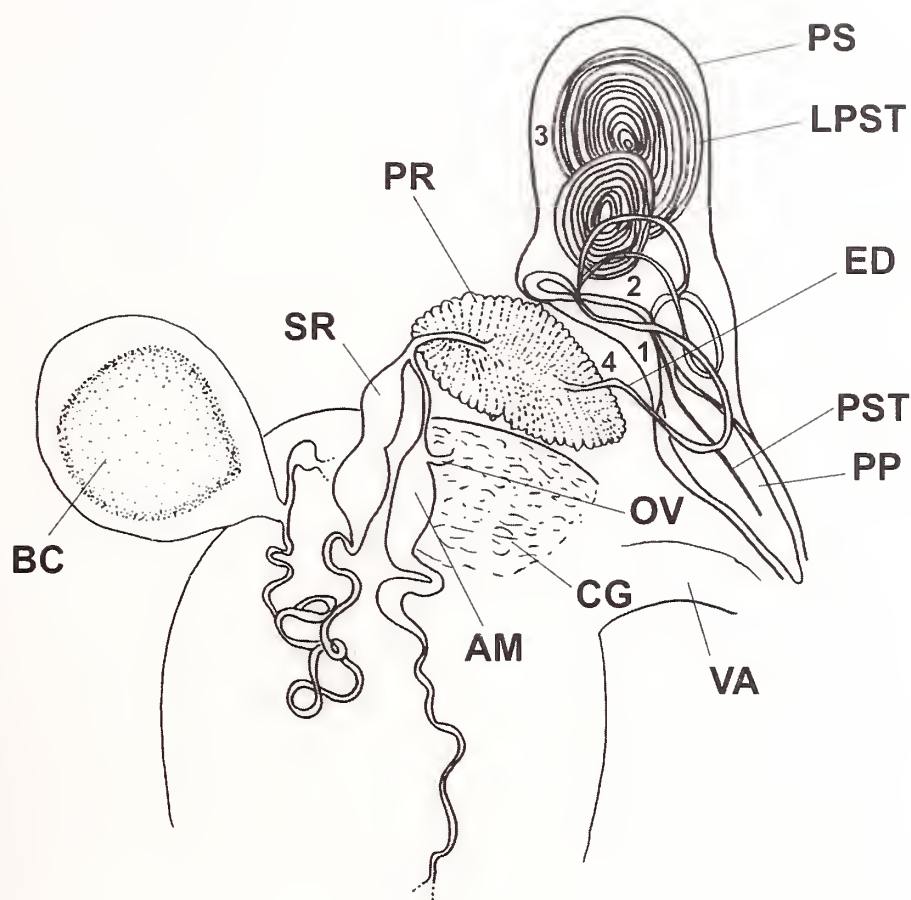


Fig. 3. Reproductive system of *P. inconspicua* MACN-in: 36985. Scale bar: 1mm. Abbreviations: AM ampulla, BC bursa copulatrix, CG capsule gland, ED efferent duct, LPST penis loop containing the cuticular stylet, OV oviduct, PP penial papilla, PR prostate, PS penial sac, PST penis (cuticular stylet), SR seminal receptacle, VA vagina. For numbers see text.

The penis is an elastic cuticular stylet, that coils in numerous helically loops (Fig. 3, number 3), that finally enters in the atrium through a penial papilla (Fig. 3, numbers 2, 1). It is difficult to find the point where the efferent duct and the penis are connected. When stretched out, the penis reaches a length of 16 and 20 cm in specimens of 45 and 80 mm length respectively. Observations of the penis under SEM reveal an external cuticle and internal cuticular stylet throughout its length (Fig. 4 A–E).

A transversal section of the penis shows that the chitinous stylet is not rounded and has a central cylindrical orifice. The shape and size of these penial stylets from two specimens examined under SEM are similar (Figs A, B, C). The width of those stylets is about 80 μ m. The penis has more than 15 roundish loops (Fig. 3, LPST, number 3), and contains the cuticular stylet all along its length (Fig. 4D). The penial stylet runs only along one fifth of the penial

cuticle (Fig. 4E). Apparently, as observed from the detail of the final portion of the efferent duct, in its portion connecting with the prostate, a central cuticular stylet inside it would be lacking (Fig. 4F).

3.2. Geographic distribution

The geographical distribution cited for *P. inconspicua* is from Cape Hatteras, North Carolina 35° N 80° W (USA) to San José Gulf 42° S 64° W (Argentina) (See Table 1, Fig. 5). Regarding the Caribbean distribution of this species, the first record from Colombia was given by ARDILA & RACHELLO (2004), with specimens from 70–150 m and an individual collected from 8–10 m, present study.

MARCUS & MARCUS (1969) recorded specimens for the first time (as *P. hedgpethi*) for Argentina (40° 32' S, 60° 19' W, 19 specimens at 57 m) and (40° 11' S, 60° 27' W,

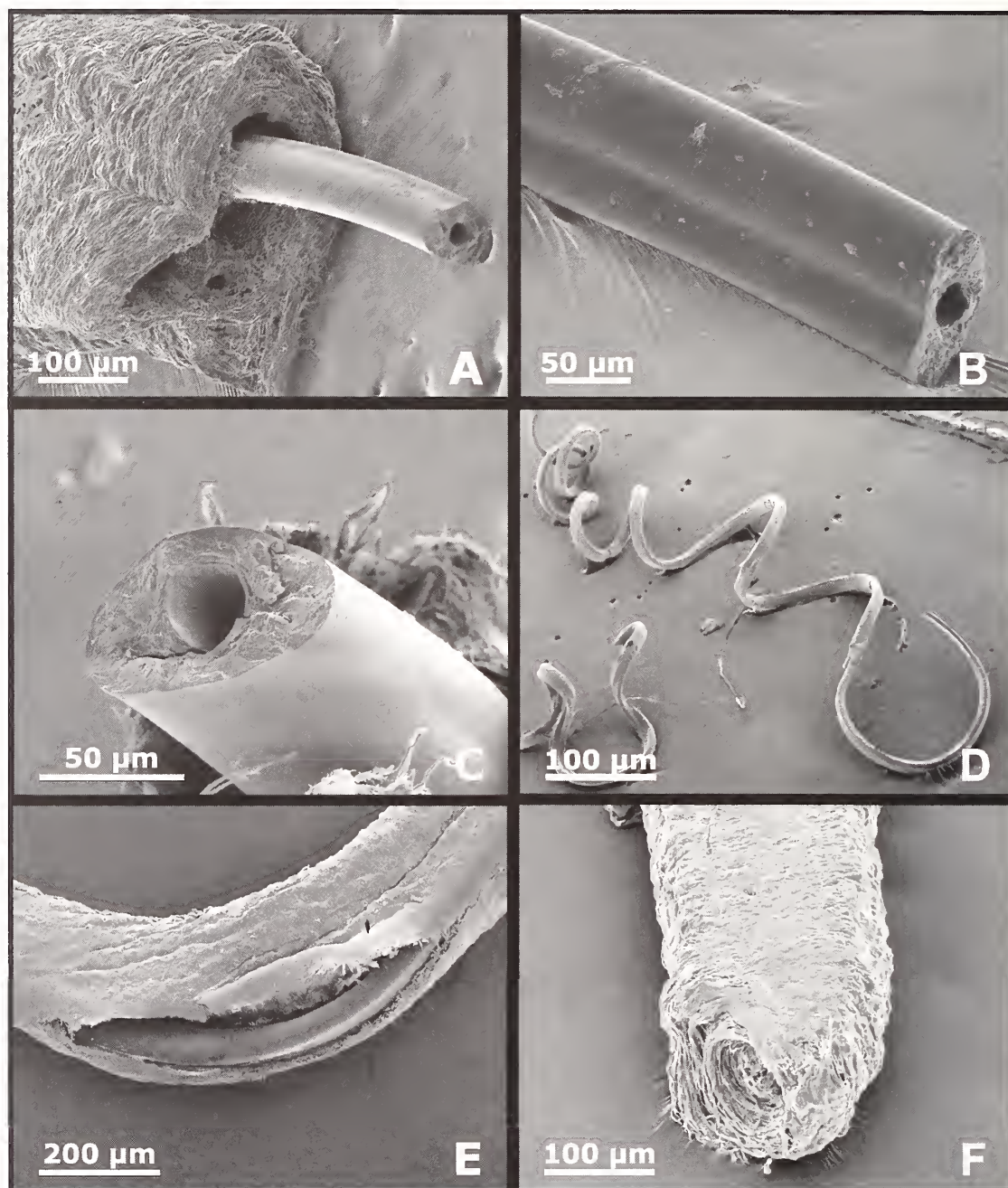


Fig. 4. SEM (critical-point-dried) of reproductive system of *P. inconspicua* (MACN-in: 36985; 37064). A. Penis, showing the external cuticle and internal chitinous stylet (MACN-in: 36985); B and C. Detail of the transverse section of the cuticular stylet of two different specimens (B, MACN-in: 36985; C, MACN-in: 37064). D. Portion of penial loop with a length of 20 cm from specimen of 80 mm in length (MACN-in: 37064). E. Dorsal view of the external cuticle, showing a portion of the cuticular stylet inside it (MACN-in: 36985). F. Detail of the region of the efferent duct that leaves the prostata (MACN-in: 37064).

7 specimens at 44 m), and their geographical range has been extended to northern Patagonia some years later for the intertidal to 8 m (MUNIAIN, 1997, present study).

MARCUS & GOSLINER (1984) cited localities from the Mediterranean Sea (Israel) and West Africa (Ivory Coast to Nigeria). Further investigations will allow testing the hypothesis of an amphiatlantic distribution.

4. DISCUSSION

As mentioned above, this work intends to serve as a starting point for further taxonomic and molecular studies involving a larger number of fresh material to verify whether this species is also present along the western coasts of Africa and the eastern Mediterranean (Israel) (amphiatlantic species), as MARCUS & GOSLINER (1984) stated, or



Fig. 5. Known distribution of *Pleurobranchaea inconspicua* Bergh, 1897, including its synonyms.

to confirm the validity of other species of the genus (e.g. *P. tarda* from Western and South Eastern Atlantic, Table 1, Fig. 5).

Thus, VALDES et al. (2006) suggest that *P. bonnieae* Marcus and Gosliner, 1984 could be a junior synonym of *P. inconspicua*. We agree with this opinion, since the description of this species is based on a single preserved and, very probably, juvenile specimen and the features suggested to differentiate it from other nominal species (*P. inconspicua* or *P. vayssierei*) are weak (presence of a penial cuticle or diameter of the base of the penis as they can be artifacts of preservation). There is no description of the living an-

imal. Besides all the facts stated above, MARCUS & GOSLINER (1984) provide unclear information about the collecting localities of their material of *P. inconspicua*, but they give a geographical range in the western Atlantic that would include the type locality of *P. bonnieae*. Another species of *Pleurobranchaea*, *P. agassizi* Bergh, 1897, would fit the geographical range for *P. inconspicua*. However, the colour of living specimens of *P. agassizi*, its bathymetric range and some anatomical differences concerning the radular teeth and the reproductive system make us consider this species as valid until additional fresh material can be studied.

External and internal characteristics of *P. inconspicua* have been described from fresh collected specimens from two distant localities of its wide distribution, as well as from preserved material. The number of pinnae of the gill and the presence of a conspicuous caudal spur are shared by all dissected specimens. All Patagonian living specimens showed the caudal spur; but it is possible that after preservation the spur is not evident, and for this reason in some descriptions it might have not been mentioned. The same hypothesis can be drawn for the posterior region of the foot sole, in which a yellow metapodial gland forms a longitudinal furrow, often visible by transparency through the skin of the dorsal side of the tail. The internal anatomy, the radula, the jaw elements and the arrangement of the reproductive organs fully agree with previous descriptions. The morphology of the internal cuticular cylindrical stylet is similar to that illustrated by MARCUS & GOSEINER (1984, fig. 1B) by optical transverse section.

An updated review of the species of *Pleurobranchaea* with details of the radular and jaw elements using SEM is needed. Although at present these characters are not considered for specific identifications, they can provide further information that can be used in the comparison of species of dubious identity. Regarding the reproductive system, the presence of a penis with cuticular stylet is an important character to separate species, but its occurrence in many species is not clear, as in *P. californica*, MacFarland, 1966 and *P. meckelii* Meckel in Leue, 1813. Some authors indicate its presence while others do not. CERVERA & GARCÍA-GÓMEZ (1988) suggest that *P. uotmec* Marcus and Gosliner, 1984 and *P. vayssierei* Marcus and Gosliner, 1984 are junior synonyms of *P. meckelii*, which agrees with a personal communication by Richard Willan. The *P. uotmec*'s holotype is from eastern Mediterranean (off Turkey) but the paratypes are from Israel (MARCUS & GOSLINER 1984), as well as one specimen attributed to *P. inconspicua* by the same authors. On the other hand, *P. vayssierei* Marcus and Gosliner, 1984 was described from a single specimen from Algiers (Western Mediterranean) among the Vayssiere's material attributed to *P. meckelii*. The diagnostic features used to erect *P. uotmec* and *P. vayssierei* seem weak to us since these species are described from few specimens and the characters vary intraspecifically (e.g. ontogeny) or could be artifacts due to preservation. Even MARCUS & GOSEINER (1984) overlooked, or were not able, to place *P. notmec* within their key to the species of Pleurobranchidae. Overall, we think that a final decision on the identity of this species will be possible only after a review of the type material and after additional fresh material is studied from the type localities areas based on both methods, morphological and molecular analyses. A future revision of type material of *P. uotmec* and *P. vayssierei*, of further specimens from the type localities, as well as of *P. inconspicua* individuals

from the Mediterranean Sea (Israel), will allow to elucidate the existence of more than one species of this genus in the Mediterranean or confirm that *P. meckelii* is the only species present in this region.

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Table 1. Diagnostic features of species of the genus *Pleurobranchaea* Leue, 1813.

Species	Geographical Distribution	Radular formula	Body Length (mm)	Cuticular style	Metapodial Spur	References
<i>Pleurobranchaea meckelii</i> (Blainville, 1825)	Type Locality: ? Mediterranean Other localities: Several Mediterranean localities (Naples, Sicily, Marseille, Genoa), Atlantic and Mediterranean Iberian Peninsula, Canary Islands, Azores Islands, Cape Verde Islands, 0–150 m.	46 X 71–0–71 50–60 X 65–55, 1.55–65 ? X 70.1, 70 ? X 70.0, 70 40–50 X 60–70.0, 70–60	up to 100	present	present	VASSIERE (1885, 1901, 1902), BERGH (1897), MARCUS & GOSLINER (1984), CERVERA & GARCIA-GOMEZ (1988), CERVERA et al. (2006)
<i>P. maculata</i> (Quoy & Gaimard, 1832)	Type Locality: ? Southern Australia Other localities: Jarvis Bay (New South West, Australia), New Zealand, Japan ?, South Africa ?, Indo West Pacific, 0–300 m.	25 X 50–0–50 40–49 X 80–0–80 40–50 X 70–80, 1.80–70	up to 50	No data	present	VASSIERE (1901), THOMPSON (1970), WILLAN (1983), MARCUS & GOSLINER (1984), BURN (1989, 2006)
<i>P. lunda</i> Verrill, 1880	Type Locality: ? Martha's Vineyard (Massachusetts) ? X 70.0, 70 Other localities: West Atlantic from Massachusetts to south of Cuba, East Atlantic from Ghana & Cape of Good Hope, South Africa 0–1450 m.		7.5–110	present	present	VASSIERE (1901), MARCUS & GOSLINER (1984)
<i>P. obesa</i> (Verrill, 1882)	Type Locality: ? 39°53'00" N, 69°50' 30" W Other localities: East Coast of North America, 353–571 m.	34 X 90–0–90 38 X 80.0, 80	40–128	present	present	BERGH (1897), VASSIERE (1901), MARCUS & GOSLINER (1984), GOSLINER (1985)
<i>P. morosa</i> (Bergh, 1892)	Type Locality: Strait of Pico-Fayal (Azores Islands), 130 m.	37 X 70–68, 0.68–70	15	No data	No data	BERGH (1892), MALAQUINAS (2001), CERVERA et al. (2006)
<i>P. agassizii</i> Bergh, 1897	Type Locality: ? Strait of Florida, Great Bahama Bank (NW Atlantic), 200–620 m.	32 X 98, 0.98 35 X 90.0, 90	20	No data	present	BERGH (1897), VASSIERE (1901), MARCUS & GOSLINER (1984)
<i>P. brockii</i> Bergh, 1897	Type Locality: ? Ambone (Indian Ocean) Other localities: Indo West Pacific, Japan, Hong Kong, South Africa, Australia 0–60 m.	40–48 X 65, 90.0, 65–90 36 X 58, 0.58 52 X 52, 0.52 35 X 65, 0.65	38–110	No data	present	BERGH (1897), VASSIERE (1901), MARCUS & GOSLINER (1984), JENSEN (1997)
<i>P. inconspicua</i> Bergh, 1897	Type Locality: Sergipe (Brazil) Other localities: North Carolina, Florida, Belize, Honduras, Venezuela, Virgin Islands, Martinique, St. Vincent & the Grenadines, Grenada, Surinam, Florida, Colombia, Argentina, Tropical West Africa (Ivory Coast to Nigeria), Israel, 0–150 m.	32–40 X 55–68, 0.55–68 34 X 72, 0.72 30 X 64, 0.64 35 X 55, 0.55	up to 60	present	present	BERGH (1897), VASSIERE (1901), ER. MARCUS (1957, 1961), NUSSEN-MEYER, 1965), ER. MARCUS (1957), EV. MARCUS & ER. MARCUS (1966, 1967b), MARCUS & GOSLINER (1984), MUNIAN (1997), ARDILA & RACHELLO (2004), VALDES et al. (2006), present study TSUBOKAWA et al. (1992)
<i>P. japonica</i> Thiele, 1925	Type Locality: ? Kōbe (Japan) Other localities: South Korea, 0–400 m.	50–80, 0.50–80	12–100	No data	No data	
<i>P. callionima</i> MacFarland, 1966	Type Locality: Golden Gate and southeast of the Farallon Light. Other localities: California, 10–470 m.	52 X 130–145, 1.130–145	up to 335	present	No data	MACFARLAND (1966), MARCUS & GOSLINER (1984), WILLAN (1987)
<i>P. angusta</i> Marcus & Gosliner, 1984	Type Locality: West Africa (17°2' S, 11° 40' E), 54 m.	40 X 70.0, 70	32	present	present	MARCUS & GOSLINER (1984)
<i>P. vassieri</i> Marcus & Gosliner, 1984	Type Locality: ? Algiers (Western Mediterranean)	35 X 65, 0.65	32	No data	present	MARCUS & GOSLINER (1984)
<i>P. babala</i> Marcus & Gosliner, 1984	Type Locality: ? Buffels Bay at Cape Point (South Africa), 10 m.	35 X 100.0, 100	70	present	No data	MARCUS & GOSLINER (1984)
<i>P. nomine</i> Marcus & Gosliner, 1984	Type Locality: ? Israel. Other localities: Eastern Mediterranean, off Turkey, 11–140 m.	50 X 80, 0.80	12–40	No data	present	MARCUS & GOSLINER (1984)
<i>P. cathartae</i> Dayrat, 2000	Type Locality: Coral Sea, Tropical Indo-Pacific Other localities: Indonesia, Philippines, Vanuato and the Marquesas, 352–760 m.	90 X 45, 0.45	52	No data	present	DAYRAT (2000)

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